

## Mating Behavior of *Peromyscus polionotus*

MICHAEL H. SMITH

STUDIES on interspecific behavioral discrimination have involved almost all of the species of *Peromyscus* in the United States (Blair and Howard, 1944; Clark, 1952; Blair, 1953 and 1954; Harris, 1954; Bradshaw, 1965; Tamsitt, 1961b; McCarley, 1964; Moore, 1965; Smith, 1965 and 1966). Unfortunately a comprehensive knowledge of this multidimensional phenomenon does not necessarily result from the inclusion of many species. Most of the existing data concern only one aspect of behavioral discrimination, the tendency to form homo- or heterospecific social aggregates under crowded laboratory conditions. The interpretation of these data usually depends upon the assumption that there is a direct relationship between the tendencies to associate and to breed with another animal. Differences in the sequence of behavior culminating in mating could prove this assumption to be in error.

Tamsitt (1961a) described mating behavior in detail for *P. comanche*, *P. nasutus*, and *P. truei* of the *P. truei* species group. The purpose of this paper is to present similar data for *P. polionotus* of the *P. maniculatus* species group and to compare these results with those of Tamsitt.

### METHODS

During 1962 and 1963, 64 pairs of mice captured in the field were used in the laboratory for breeding stock. Occasionally, one escaped or died and had to be replaced; additional pairs were added later to the colony. Four Florida subspecies were represented: *P. polionotus subgriseus* from Ocala National Forest, *P. p. phasma* from Anastasia Island, Saint Johns County, *P. p. leucocephalus* from Santa Rosa Island, Okaloosa County, and *P. p. rhoadsi* from Archbold's Biological Station, Highlands County.

The mice were kept in cages similar to those described by Layne (1958); the sides were made of one-quarter inch hardware cloth and the wood tops were removable. Each cage was placed on a tray covered with sawdust. The ambient temperature in the laboratory was usually  $24 \pm 2^{\circ}$  C; occasionally it varied as much as  $5^{\circ}$  C. Relative humidity was measured with a sling psychrometer

at different times during the day and night; it varied from 54 to 84 per cent. Overhead fluorescent lights were automatically turned on at 0630 and off at 2030; no outside light entered the room. Purina laboratory chow and water were supplied ad lib.

Mating was regularly accompanied by sound and occurred in the evening while the lights were still on in the colony room. Detailed notes were made on 16 different pairs of *P. p. subgriseus* for a total of 25 matings. Additional scattered observations were made on the other three subspecies. One pair was observed at a time. All of the matings occurred during the post-partum heat. The cages were checked in the morning for new-born litters, and if present, observations were begun that night 30 minutes before the overhead lights went off. A reflector lamp with a 100-watt red light located eight to ten feet from the cage was used after the room became dark.

Sometimes the mice appeared to have no interest in breeding. In a majority of these cases, however, copulation occurred within a few minutes after the mice were given a ball of cotton about 3 cm in diameter. Thirteen of the 25 matings occurred with the previous litter present and 12 without it. Four additional matings were observed in a wooden cage (50 cm high, 45 cm wide, 75 cm long) with a glass front and one-quarter inch hardware cloth on the back. The large cage was used because Tamsitt (1961a) suspected that certain aspects of the breeding behavior might have been caused by the small size of his cages.

## RESULTS

Mating of the old-field mouse varied from pair to pair and with the number of copulations that took place on the same evening (Fig. 1; Table 1). The sequence usually associated with the first few copulations will be presented first and the variation from this sequence will follow.

The female initiated mating by positioning herself in front of the male. Her ears were erect, the tail was low, and the body was held high. The white underparts of the side of her body next to the male were displayed, and the eye on the same side was slightly closed. She moved forward displaying one side of her body, and just before making contact, lowered her body and turned her head upward and to the side, thus exposing her white throat. The male



tight circle in front of the male with her head, tail, and body close to the floor. In the large cage, the female ran back and forth on the floor in front of the male. If the male did not chase the female, she repositioned herself in front of him and repeated the entire sequence.

The naso-anal contact became so vigorous in some cases that the female was pushed forward. In other instances, the male repeatedly moved its head upward after placing it under the female's anal region. This movement elevated the posterior half of the female's body 3 to 5 cm exposing her white belly. The male frequently tried to mount the female if she slowed down slightly. Successful mounting occurred only when the female came to a complete stop. At this moment she extended her body forward, angled the tail laterally, arched her back, and thus raised the exposed perineum. The male mounted by extending his body over hers and then grasped her body in the region of the diaphragm with his front legs. Intromission consisted of a single forward thrust of such force that the female was normally pushed forward. The female was never heard squeaking during intromission. After the forward thrust, the male relaxed its grip of the female. The male always lifted one leg as he drove the penis forward. Occasionally, the other leg was also lifted at the end of the forward thrust, and thus, the male rode on the back of the female. In these cases, the male slowly fell off the female onto his side or back. If one foot remained on the floor, the male dismounted as the female moved forward. The male then sat upright on the hind legs and tail, bent its head toward the floor, pulled sheath of the penis back with the forepaws, and took the withdrawn penis into the mouth and washed it. At the same time, the female licked her genitalia from a similar position. Both sexes went through a complete "wash", which includes the entire body and tail, following the cleaning of the genital area. The "wash" of the female was of shorter duration than that of the male. She went back to the nest, which contained the newborn young, and then ate or drank before initiating the next mating. The male was frequently still cleaning his fur when the female repositioned herself in front of him. Mice always copulated many times during the course of an evening (Table 1). No conspicuous marking behavior, such as urination or dragging the genital region on the floor, was observed.

TABLE 1

Mating data for laboratory-reared *Peromyscus polionotus subgriseus*

Number of pairs observed	16
Successful matings	25
Mean number of mounts per mating	49.8
Mean number of thrusts per mating	45.6
Intromissions per total mounts	91.6%
Mean number of washing of penis by male per mating	23.1
Mean observation time in minutes per mating	152.6

Copulations were not randomly distributed over time but occurred in groups (or series) with a greater amount of time between groups than between successive copulations. Between each series of copulations the animals rested and showed no sexual behavior for at least three minutes. The male frequently lay facing the nest from the farthest possible point in the cage, keeping his body and tail flat on the floor, ears erect, and limbs extended in a position similar to that used by heat-stressed animals. The female usually stayed in the nest with the young mice. As the length of the period of mating increased, both mice spent more time drinking, eating, urinating, and defecating during the rest periods. The number of series of copulations per mating period ranged from six to twelve and averaged 9.2. The mean number of copulations per series decreased and the length of the rest period between each series increased as the number of copulations completed that night increased. The mean number of copulations for the first series was 6.8 and for the last series was 2.6. The average length of the rest period between the first and second series was 3.8 minutes, and it was 15.3 minutes before the last series.

Mating behavior on any one evening gradually changed as the total number of completed copulations increased. The male responded to changes in the female's behavior more quickly than before. Grooming and smelling of the genital region were frequently deleted. The male often started chasing the female without being approached by her. The washing of the penis occurred less frequently, and the partial wash of the head and ears were more common than the complete performance. The female cleaned her genitalia less frequently.

In almost all of the later matings the male took the initiative. He would approach the female head on while she was in the nest. The female would frequently assume an upright posture, and the male would attempt to push the female over on her back and wash her white belly. The female uttered frequent, high-pitched sounds during the initial advances of the male and occasionally while she was on her back. When the female righted herself, she would run out of the nest with the male chasing after her and the normal sequence of events occurred.

Sometimes, when the female resisted the male's efforts, the male picked up a new-born animal and carried it out of the nest. The female immediately retrieved the young animal and after depositing it in the nest, the female would run from the nest with the male following. The male frequently attempted to mount the female while she was retrieving the young animal but was never successful. Half of the males picked up young animals and moved them out of the nest during their mating behavior. The other males concentrated their efforts on the females. New-born animals were displaced several times from their nest by one male the first time it was observed and not at all during the second period of observation. The general scheme of this male's mating behavior was similar on both occasions except in this one regard.

Females gradually became more aggressive and drove their mate and previous litter from the nest when they were still present. The female frequently lunged at the male and tried to bite him. Eventually, the male left the female alone in the nest and mating ceased. In some cases, the female left her previous litter in the nest although she drove her mate out. The period during which the previous litter and/or the adult male were kept out of the nest varied from several hours to several days.

The young animals from the previous litter were allowed only restricted movements during the mating of their parents. Initially, they spent most of their time in the nest but were later found eating and drinking near the water bottle. As the female approached, they would run back to the nest. Except in one case, the young animals played no direct part in the mating behavior. One juvenile male entered into the chasing of the female. The juvenile male never attempted to mount his mother or make any kind of physical contact with her. He ran behind his father and frequently tried

to mount him. The adult male paid little attention to the activity of the juvenile, but the female frequently lunged at him and eventually chased him back into the nest with the other young mice.

On four occasions, mating was observed when there was more than one adult male in the cage. Usually only one male bred with the female. The others either remained in one corner of the cage or they attempted to mount the male that chased the female. Once two males alternately tried to mount a female, but one repeatedly failed because the female never stopped and arched her back when he tried to mount.

The only consistent difference observed in the mating behavior of the several subspecies was the lack of squeaking by females of *P. p. phasma*.

#### DISCUSSION

As pointed out by Smith (1966), the normal social unit in this species is an adult male and female with or without young. Females are normally dominant over their mates and play a major role in the process of pair formation and maintenance of the pair bond. No other species of *Peromyscus* is known to be as social as *P. polionotus*. A proper interpretation of the behavior of the old-field mouse and its comparison with that of other species in this genus can only be made when these unique characteristics of the species are kept in mind.

Mating was the result of a series of social interactions in which the female at first played a submissive role and then later a dominant one. The change was gradual and was accompanied by an increase in the amount of initiative shown by the male. Squeaking by the female only occurred in ambivalent situations characterized by both avoidance and approach tendencies. Once the female started to run in front of the male or attacked him, she would stop squeaking. Display of the white underparts of the female's body was also a part of her submissive behavior. Reversal of the normal social hierarchy seemed to be a necessary prerequisite for the completion of mating. The re-establishment of the female's dominance over the male was correlated with the cessation of mating.

The six phases of the mating pattern described by Tamsitt (1961a) for the *P. truei* species group were also evident in the behavior of *P. polionotus*. They were "(1) initiation of courtship

by the female, (2) circling of the female before the male, (3) posturing by the female before the male, (4) mounting by the males, (5) thrust-intromission by the male, and (6) dismounting by the male." Of these arbitrary divisions only circling in front of the male by the female was considered to be a laboratory artifact caused by the small cage size. The essential part of the circling was probably the movement away from the male, or fleeing; this being interpreted as submissive behavior.

The overall similarity of the mating patterns was probably due to the close phylogenetic relationship of the mice. Both of the species groups belonged to the subgenus *Peromyscus*. Despite the similarity, a detailed comparison of the results also revealed some consistent differences.

Only the females squeaked, but they did so at different times. Those in the *P. truei* group usually squeaked once during intromission; *P. polionotus* females were quiet at this time but vocalized during their interactions with the males prior to mounting. However, this behavior was not an essential part of mating since the *P. p. phasma* females always remained silent and the females of the *P. truei* group occasionally did likewise. These sounds may be used for species recognition in *P. polionotus* but were more likely a sign of submission by the female. The silence of the *P. p. phasma* females may be related to the open habitat on the beach dunes where they are found, but *P. p. leucocephalus* females vocalized occasionally, although not as frequently as some of the other subspecies. The latter subspecies was also collected on the sand dunes. Silence may be selectively advantageous in open habitats, because certain predators can use sounds to locate their prey.

Males of all of the subspecies of *P. polionotus* were observed carrying newborn young out of the nest. This behavior was not mentioned for *P. truei* by Tamsitt, but he did not observe mating during the post-partum heat so there were no young animals present. Handling of the young by the male, however, was not an essential part of mating. Some of the males never exhibited this behavior, while others did so only during one of the several observed mating periods.

The nest acts as a focal point around which the mice center their mating behavior. This may be due to a conflict between mating behavior and maternal behavior in the female, or it indicates



that mating normally takes place within the burrow in the field. A third alternative is that it is related to the small size of the cages. The last does not seem likely since the mice used their nest in the big cage just as often as in the small ones. By mating underground the mice would not be as susceptible to predation. The old-field mice would be perfectly safe if they left the entrance to their burrow sealed as they do during the day (Smith, 1966).

The last and perhaps most important difference is the lack of conspicuous marking behavior by the *P. polionotus* females. In the *P. truei* group females dragged the perineal region on the floor propelling themselves by movements of the forelimbs. Nothing even remotely similar to this was observed in *P. polionotus*. Tamsitt interpreted the females behavior as functioning in depositing olfactory stimuli for the male. After being stimulated the male would make contact with the female and a series of epimeletic activities would ensue, their function being to condition the mice to each other's presence. This type of conditioning was not necessary in *P. polionotus* because of the prior formation of the pair bond (Smith, 1966). The various characteristics of the mice that contribute to the formation of the pair bond in *P. polionotus* were probably more important than the minor variations encountered in their mating behavior as compared with that of the *P. truei* group. Of course these same characteristics can be used for discrimination during mating, but if they were they did not seem to be emphasized to the same degree in the different species of mice. Recognition was already established before mating started in *P. polionotus*.

#### SUMMARY

Mating is the result of a series of social interactions in which the female at first plays a submissive role and then later a dominant one. Six phases are recognized in the mating behavior of *P. polionotus*: (1) initiation of courtship by the female, (2) running away by the female, (3) posturing by the female before the male, (4) mounting by the male, (5) thrust-intromission by the male, and (6) dismounting by the male. These are essentially the same as those described by Tamsitt (1961a) for the *P. truei* group. There are differences in the mating sequence of the two types of mice, but only one of these seems to be essential to the completion of mating. This is the marking behavior of the females of the *P. truei* group, an action which

was not observed in *P. polionotus*. One of the functions of this behavior is probably species recognition, and since recognition is established prior to mating in *P. polionotus*, marking would be superfluous in this species.

#### ACKNOWLEDGMENTS

I would like to thank Dr. E. G. F. Sauer for his patience and guidance as chairman of my Ph.D. committee. Drs. R. Beyers, D. Coleman, and F. Golley critically read the final draft of the paper, and my wife, Irma Smith, assisted me in various ways. A grant-in-aid from Sigma Xi and support from the Department of Zoology at the University of Florida helped finance the study. Preparation of the manuscript was aided by AEC Grant AT(38-1)-310 and NSF Grant GB5140. To all of the above I express my sincere appreciation.

#### LITERATURE CITED

- BLAIR, W. F. 1953. Experimental evidence of species discrimination in the sympatric species, *Peromyscus truei* and *P. nasutus*. Amer. Natur., vol. 87, pp. 103-105.
- . 1954. Tests for discrimination between four subspecies of deer mice (*Peromyscus maniculatus*). Texas Jour. Sci., vol. 6, pp. 201-210.
- AND W. E. HOWARD. 1944. Experimental evidence of sexual isolation between three forms of mice of the cenospecies *Peromyscus maniculatus*. Contrib. Lab. Vert. Biol. Univ. Michigan, vol. 26, pp. 1-19.
- BRADSHAW, W. N. 1965. Species discrimination in the *Peromyscus leucopus* group of mice. Texas Jour. Science, vol. 17, pp. 278-293.
- CLARK, W. K. 1952. Isolating mechanisms, competition and geographic variation of the *Peromyscus boylei* group in Oklahoma and Texas. Unpubl. Ph.D. dissertation, Univ. Texas, 102 pp.
- HARRIS, VAN T. 1954. Experimental evidence of reproductive isolation between two subspecies of *Peromyscus maniculatus*. Contrib. Lab. Vert. Biol. Univ. Michigan, vol. 70, pp. 1-13.
- LAYNE, J. N. 1958. A simple and inexpensive small animal cage for laboratory use. Turtlox News, vol. 36, pp. 208-209.
- MCCARLEY, H. 1964. Ethological isolation in the cenospecies *Peromyscus leucopus*. Evolution, vol. 18, pp. 331-332.
- MOORE, R. E. 1965. Olfactory discrimination as an isolating mechanism between *Peromyscus maniculatus* and *Peromyscus polionotus*. Amer. Midl. Natur., vol. 73, pp. 85-100.

- SMITH, M. H. 1965. Behavioral discrimination shown by allopatric and sympatric males of *Peromyscus eremicus* and *Peromyscus californicus* between females of the same two species. *Evolution*, vol. 19, pp. 430-435.
- . 1966. The evolutionary significance of certain behavioral, physiological, and morphological adaptations of the old-field mouse, *Peromyscus polionotus*. Unpubl. Ph.D. dissertation, Univ. Florida 187 pp.
- TAMSITT, J. R. 1961a. Mating behavior of the *Peromyscus truei* species group of white-footed mice. *Amer. Midl. Natur.*, vol. 65, pp. 501-507.
- . 1961b. Tests for social discrimination between three species of the *Peromyscus truei* species group of white-footed mice. *Evolution*, vol. 15, pp. 555-563.

*Institute of Ecology and Department of Zoology, University of Georgia (mailing address: Savannah River Ecology Laboratory, c/o U. S. Atomic Energy Commission, SROO, Box A, Aiken, South Carolina 29801).*

Quart. Jour. Florida Acad. Sci. 30(3) 1967 (1968)